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Gizzard and other lean mass components increase, yet Basal Metabolic Rates decrease, when red knots *Calidris canutus* are shifted from soft to hard-shelled food

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Piersma, T., Gessaman, J. A., Dekinga, A. and Visser, G. H. 2004. Gizzard and other lean mass components increase, yet Basal Metabolic Rates decrease, when red knots *Calidris canutus* are shifted from soft to hard-shelled food. – J. Avian Biol. 35: 99–104.

We measured basal metabolic rate (BMR), body mass, lean mass, and gizzard mass of captive red knots *Calidris canutus islandica* maintained on a trout chow diet (soft-texture, low ash and water content) for several years and then shifted to small mussels *Mytilus edulis* (hard-texture, high ash and water content). During a 3-week period of feeding on mussels, body mass, lean mass, and gizzard mass increased 7.3 g (+7%), 10.5 g (+12%), and 4.9 g (+213%), respectively, yet BMR decreased from 0.96 to 0.89 W (–8%). Under the new mussel regime, red knots must have reduced the metabolic intensity of some of the tissues. This suggests that the experimental red knots experienced the transition to a mussel diet as stressful and energy limiting, resulting in an energy-saving strategy by reducing BMR in spite of hypertrophy of the gizzard and other organs.

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The Basal Metabolic Rate (BMR) has long been regarded as a primary metabolic adaptation of homeotherm vertebrates (see McNab 2002). Increasingly it has become clear, however, that BMR is a function of several basic physiological variables which themselves may be under direct selection. These factors include body temperature (Reinertsen 1983), metabolic hormone levels (Stokkan 1994, Kersten et al. 1998) and body composition including organ sizes (Daan et al. 1990,

Piersma 2002). Here we report on intra-individual changes in BMR which suggest that food stress directly affects mass-specific BMR. To the best of our knowledge this has not previously been proposed.

The digestive tract of red knots *Calidris canutus* is flexible, and can easily be adjusted to the 'hardness' and quality of a diet that normally consist of molluscs swallowed whole (Dekinga et al. 2001, van Gils et al. 2003, Battley and Piersma 2004). Piersma et al. (1993)

were the first to report a severe reduction in gizzard mass for red knots that ate soft food in captivity. When acclimatized to hard-shelled prey, a soft diet such as trout chow induces gizzard mass reductions of about 50% within a week. Such changes are reversible, and decreases and increases occur at about the same rate (Dekinga et al. 2001, van Gils et al. 2003).

Differences in the digestive organ size of red knots associated with diet have been correlated with differences in BMR (Piersma et al. 1996). The BMR of two subspecies (*C. c. islandica* and *C. c. canutus*) maintained on a soft diet of trout pellets during long-term captivity was lower than the values of their free-living counterparts that predominately ate hard-shelled molluscs (Piersma et al. 1996). Nearly all the variation in the average BMR between these captive and wild knots was explained by the corresponding variation in lean mass. Differences between BMR of wild and captive birds seemed to be due especially to mass differences in the nutritional organs, notably the gizzard and the intestine. The two organs comprised 12% of lean dry mass in wild birds and 5.5% in captive birds. As organ masses and BMR were not measured in the same individuals, but rather on small subsets of birds from two geographical areas (The Netherlands vs West and South Africa) and two 'treatments' (wild vs captive birds), this conclusion remains tentative.

We compare BMR of captive individuals maintained on trout pellets with their BMR after three weeks on a diet of bivalves. Following this switch we expected to find an increase in gizzard size, lean mass and BMR. Measurement of the Respiratory Quotient enabled us to see if changes in diet, induced changes in the metabolic substrates used.

Methods

Experimental animals and diet

This study was carried out during November and December 2000 on 7 adult knots (6 males and 1 female) of the subspecies *C. c. islandica*. All birds were captured at the Dutch Wadden Sea and had been maintained in captivity for several years. Males were captured in November 1994 (5) and in October 1995 (1). The female was captured in February 1997.

During our study the birds were kept together in one indoor aviary (4.5 m × 1.5 m × 2.3 m high) at the Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands, at an average air temperature of 12°C and a Light:Dark cycle of 10:14. The floor of the aviary was continuously flushed with salt water to prevent infections and skin lesions caused by dry feet. Birds had fresh water to drink and had been fed *ad libitum* trout chow since their arrival in captivity (see Dietz et al. 1999b for the long-term trajectory of gizzard size

following a shift to such a diet). After two successive measurements of BMR, approximately a week apart, birds were switched to a diet of blue mussels *Mytilus edulis* for three weeks, prior to another measurement of BMR. The small, 5–15 mm long, mussels offered were collected at the basalt groynes (wave breakers) on the North Sea beach of Texel. Dense mussel clusters were broken up and the loose mussels rinsed and cleaned before being given to the birds.

Respirometry

BMR was measured using a respirometry system for monitoring oxygen consumption (VO_2) and carbon dioxide production (VCO_2). The lowest 60-min of energy metabolism over a 16 h period (from around 16.00 h to around 08.00 h) was taken as BMR. Six hours prior to the beginning of a 16 h BMR measurement period, a bird was removed from the aviary and placed in a cardboard box without food to create a post-absorptive condition. Subsequently, the bird was weighed to the nearest 0.1 g before being placed in darkness within a PVC chamber.

The chambers were placed in a temperature-controlled cabinet set at 20°C, i.e., within the thermoneutral zone of red knots (Piersma et al. 1995). Dried outside air was pumped into the sealed chambers. Flow rates of air entering a chamber were controlled at around 50 l h⁻¹ and were measured with mass flow controllers (Model 5850S, Brooks Instruments, Veenendaal, The Netherlands), which were calibrated using a Bubble-O-Meter (LaVerne, California). With these flow rates, the average hourly percent CO_2 in a chamber during BMR measurements averaged 0.26% (SD = 0.02). Air leaving the chamber was dried with a molecular sieve (granules approximately 2 mm; Merck). Oxygen and carbon dioxide concentration of dried inlet and outlet air was measured with a Servomex paramagnetic oxygen analyzer (Model 4100, with an accuracy of >98%) and a Servomex IR carbon dioxide analyzer (Model 1400, with an accuracy of 97.4%), respectively. Both gas analyzers were calibrated daily using pure nitrogen as a low reference. Dry air (assumed to contain 20.95% O_2) and a standard gas of 0.502% CO_2 were used as the high references for the O_2 and CO_2 analyzers, respectively. The volume fractions of O_2 and CO_2 in the inlet air ($F_{\text{I}\text{O}_2}$ and $F_{\text{I}\text{CO}_2}$, respectively) were monitored for 5 min every hour, and the volume fractions of O_2 and CO_2 in the outlet air ($F_{\text{E}\text{O}_2}$ and $F_{\text{E}\text{CO}_2}$, respectively) were then monitored for the remainder of the hour. Average hourly VO_2 and VCO_2 over the 16-h period were compiled from $F_{\text{E}\text{O}_2}$ and $F_{\text{E}\text{CO}_2}$ sampled every 30 s. At the end of the metabolic measurement the bird was again weighed to the nearest 0.1 g.

The limitations of our system required that VO_2 and VCO_2 be computed using an assumed Respiratory Quotient (RQ) or a close approximate measure of RQ (RQ_{ap}). We used the latter approach. We computed the rate of oxygen consumption (VO_2) and carbon dioxide production (VCO_2 , in $1 \text{ CO}_2 \text{ h}^{-1}$ or day^{-1}) with equations 6 and 7, respectively, derived from the fundamental relationships shown in equations 1 to 5.

$$\text{VO}_2 = \text{V}_1 \text{F}_1 \text{O}_2 - \text{V}_\text{E} \text{F}_\text{E} \text{O}_2 \quad (1)$$

$$\text{VCO}_2 = \text{V}_\text{E} \text{F}_\text{E} \text{CO}_2 - \text{V}_1 \text{F}_1 \text{CO}_2 \quad (2)$$

$$\text{V}_\text{E} = \text{V}_1 - \text{VO}_2 + \text{VCO}_2 \quad (3)$$

$$\text{VO}_2 = \text{VCO}_2 / \text{RQ} \quad (4)$$

$$\begin{aligned} \text{Assuming that } \text{RQ} \sim \text{RQ}_{\text{ap}}, \text{ then } \text{RQ}_{\text{ap}} \\ = (\text{F}_\text{E} \text{CO}_2 - \text{F}_1 \text{CO}_2) / (\text{F}_1 \text{O}_2 - \text{F}_\text{E} \text{O}_2) \end{aligned} \quad (5)$$

$$\text{VO}_2 = \text{V}_1 (\text{F}_1 \text{O}_2 - \text{F}_\text{E} \text{O}_2) / (1 - \text{F}_\text{E} \text{O}_2 (1 - \text{RQ}_{\text{ap}})) \quad (6)$$

$$\begin{aligned} \text{VCO}_2 = \text{V}_1 (\text{F}_\text{E} \text{CO}_2 - \text{F}_1 \text{CO}_2) / (1 \\ + \text{F}_\text{E} \text{CO}_2 (1 / \text{RQ}_{\text{ap}} - 1)) \end{aligned} \quad (7)$$

where V_1 and V_E are the flow rates (in 1 h^{-1}) of air entering and exiting the bird chamber, respectively. The energy equivalent of oxygen consumption for BMR measurements was estimated (Gessaman and Nagy 1988) using a constant energy equivalent of $20 \text{ kJ l}^{-1} \text{ O}_2$ (as in Piersma et al. 1995, Weber and Piersma 1996, Piersma et al. 1996). We then converted rate of energy metabolism to Watts: 0.2777 kJ h^{-1} per W.

Measurement of lean body mass

We used the ^{18}O dilution method (Speakman et al. 2001) to estimate the total amount of lean wet mass of each bird during the respiration measurement. Each bird was first weighed to the nearest 0.1 g, and subsequently intraperitoneally injected with a dose of about 0.40 g of a water mixture with an ^{18}O concentration of 44.1% (based on the supplier's information, but verified by us using the principle of isotope dilution, Visser et al. (2000b)). The exact quantity of each dose was determined by weighing the syringe to the nearest 0.1 mg before and after administration. Next, each bird was kept individually in a well-ventilated cardboard box for equilibration of the dose. After 1 h the brachial vein was punctured with a sterile needle for a blood sample of about 0.3 ml that was stored in a 1-ml quartz vial. Thereafter the bird was placed in the respiration chamber. At the end of the measurement period the bird was taken out of its chamber, and its body mass measured again. We also collected blood samples of 4 animals prior to administration of the dose, to determine the natural ^{18}O content in the birds' body water pools (see below). Blood samples were stored at 4°C until analysis at the Centre for Isotope Research in Groningen

following the analytical procedures detailed by Visser et al. (2000a).

The size of the body water pool (TBW, g) at the start of the respiration measurement was calculated for each bird on the basis of the principle of isotope dilution, i.e., on the basis of the determination of its ^{18}O dilution space. The quantity (Q_d , moles) and the ^{18}O concentration (C_d , 44.1 atom percent) of the dose are known, as well as the ^{18}O concentration in the bird's body water pool prior to the administration (C_b , determined to be on average 0.1992 (SD = 0.00042, $n = 4$) atom percent), and the measured individual-specific ^{18}O concentration after equilibration of the dose (C_i , atom percent):

$$\text{TBW} = 18.02 \cdot \text{Q}_\text{d} \cdot (\text{C}_\text{d} - \text{C}_\text{i}) / (\text{C}_\text{i} - \text{C}_\text{b}) \quad (8)$$

This method has been referred to as the 'plateau method' (Visser et al. 2000b, Speakman et al. 2001).

Based on carcass analyses, the ratio of TBW to lean body mass is 0.69 (T. Piersma unpubl. data). Assuming that the fractional lean body mass value remained constant throughout the 16 h of confinement, lean body mass was calculated from the average of body masses at the start and end, and TBW measured at the start of the experiment.

Ultrasonography

Measurements were done with a Pie 200 ultrasound instrument with a 7.5 MHz linear probe (Pie Medical Benelux BV, Maastricht, The Netherlands) using an ultrasonic gel for coupling the probe to the surface of the animal. The images were printed on a Mitsubishi video copy processor, Model P90E. Width of the gizzard was measured by placing the probe transversely on the belly of the bird at an angle of approximately 45° just below the rib case (Dietz et al. 1999a). Measurements were done blindly, with the observer being unaware of the identity and body mass of the bird. Prior to the experiment, calibration curves were made for the observer (AD) using 21 dead red knots with a wide range of gizzard sizes. Gizzard width was used as an estimate of gizzard mass, because gizzard width appeared to be the most reliable predictor of gizzard mass for the observer (Dietz et al. 1999a). The gizzard width measurements were converted to gizzard masses as follows:

$$\text{Gizzard mass (g)} = 7.88 \times \text{gizzard width (cm)} - 5.35 \quad (9)$$

Results

All results are summarized in Table 1. Total body mass increased with 7.3 g (+7%) from 101.9 g (SD = 3.6) to 109.2 g (SD = 3.4) after the shift from trout chow to mussels. Whereas average total lean mass increased with 10.5 g (+12%) from 88.0 g (SD = 5.2) when feeding on

Table 1A. Basic data for the seven individual red knots examined for various physiological variables before and after a three-week adjustment to a mussel diet after a long-time exposure to a diet of pellets.

Variable	Diet	ID						
		1	2	3	4	5	6	7
Body mass (g)	Pellet	107.0	101.6	98.8	101.5	106.8	99.7	98.1
	Mussel	108.0	111.0	105.0	109.0	105.3	113.9	112.0
Lean mass (g)	Pellet	97.8	88.0	84.8	85.3	85.9	90.2	84.3
	Mussel	101.7	95.5	99.8	94.8	92.1	108.3	97.1
Gizzard mass (g)	Pellet	2.53	1.58	1.82	2.61	2.45	2.69	2.37
	Mussel	6.55	6.55	6.71	7.42	8.12	6.63	8.28
BMR (W)	Pellet	0.91	0.98	0.87	0.93	0.94	1.09	1.02
	Mussel	0.78	0.87	0.82	0.86	1.00	1.00	0.87
RQ _{ap}	Pellet	0.71	0.70	0.67	0.70	0.69	0.72	0.73
	Mussel	0.69	0.66	0.66	0.70	0.64	0.67	0.64
Rate of mass loss (g 100 g ⁻¹ day ⁻¹)	Pellet	7.1	8.1	8.4	7.3	9.9	9.7	8.7
	Mussel	11.2	10.8	11.7	5.3	12.6	10.4	23.9

Table 1B. Results of paired t-tests for the differences in average physiological traits during the two diet treatments.

Variable	Averages		Differences	
	Pellet diet	Mussel diet	paired-t	P-value
Body mass (g)	101.93	109.17	- 3.2	0.018
Lean mass (g)	88.04	98.47	- 5.4	0.002
Gizzard mass (g)	2.29	7.18	- 17.4	< 0.0001
BMR (W)	0.963	0.886	2.9	0.026
RQ _{ap}	0.703	0.666	3.23	0.018
Rate of mass loss (g 100 g ⁻¹ day ⁻¹)	8.46	12.27	1.86	0.112

trout chow to 98.5 g (SD = 5.2) after three weeks on mussels, gizzard mass increased by 4.9 g (+213%) from 2.3 g (SD = 0.4) to 7.2 g (SD = 0.8). The double measurement of BMR values when the birds were still on trout chow showed BMR to be highly repeatable ($r = 0.974$, $P < 0.0001$). BMR of red knots maintained on trout chow was 0.96 W (SD = 0.05), which decreased significantly to 0.89 W (SD = 0.08) after the shift to mussels (-8%). RQ_{ap} averaged 0.70 during the respirometry fast while on the trout chow regime, and 0.67 during the mussel regime. During BMR measurements (no food ingested), red knots on the trout chow and mussel diets showed rates of mass loss of 8.5 and 12.3 g 100 g⁻¹ day⁻¹, respectively.

Discussion

Dekinga et al. (2001) found that gizzard masses of 11 red knots that had been maintained on trout chow for more than a year averaged 2.05 g and increased to 6.26 g after three weeks of feeding on blue mussels. At the same time average body mass increased from 113 to 130 g, gizzard mass gain thus accounting for about 25% of the body mass gain. In our study, gizzard mass increased from 2.3 g to 7.2 g, implicating that 67% of the overall gain in body mass could be attributed to gizzard hypertrophy. As the lean mass increased 10.5 g, which is 5.6 g more

than the gizzard mass gain of 4.9 g, one or more other organs (most likely the intestine; Battley and Piersma 2004) were also upregulated.

The BMR values reported sit comfortably within the range of values expected for pellet-eating captive red knots of their mass (Piersma et al. 1995, 1996, Weber and Piersma 1996). Nevertheless, based on studies such as Lindström and Kvist (1995), Piersma et al. (1996) and Hammond et al. (2000), we had expected that a shift from soft to hard-shelled food, inducing hypertrophy of the digestive tract would lead to a marked increase in BMR. Instead, BMR decreased, despite a lack of change in Daily Energy Expenditure as measured by respirometry in the same groups of birds (J. A. Gessaman, A. Dekinga and T. Piersma unpubl. data). The increase in both body and lean mass concomitant with a decrease in BMR indicates that BMR is not always a positive function of either total body mass, lean mass or specific-organ masses. The latter is found in many (e.g., Williams and Tieleman 2000, Battley et al. 2001, and see review by Piersma 2002), but not all studies. For example, the analysis by Kersten et al. (1998) indicated that the lower BMR of shorebirds wintering in the tropics compared with temperate latitudes, and specifically for a comparison within red knots, cannot only be due to lower lean body masses but must involve a change to lower metabolic intensities of some organs as well. In the case of the zebra finches *Taeniopygia guttata* made to

work hard for their food by Deerenberg et al. (1998), a 24% decrease in BMR under the harsh regime was also suggested to involve a lowering of the average metabolic intensity of the lean tissues.

Given the difficulty and reluctance of captive red knots fully adjusted to trout chow to make a shift to hard-shelled mollusc prey (Piersma et al. 1993), we propose that the three-week period of acclimatization to the new mussel diet was not enough, and that in the context of their captive environment where they have been 'spoiled', red knots still experienced their new diet as a stress factor. The lower RQ_{ap} and the higher rate of body mass loss during the fasting period after the shift to a mussel diet (both indicating an increasing use of protein (lean mass) and the conversion of protein to glucose by gluconeogenesis; see Kleiber 1961, Gessaman 1987) are consistent with the well-established phenomenon that during starvation birds have higher circulating levels of the stress hormone corticosterone and use protein as fuel (e.g., Cherel et al. 1988).

Thus, when faced with a food stress such as forced feeding on difficult and unwelcome prey types, birds may resort to energy saving mechanisms that involve reductions in average lean tissue metabolism. In red knots, this could occur when birds return to temperate coastal wetlands from their tundra breeding grounds in late summer and have to make the shift from relatively soft-bodied arthropods to hard-shelled molluscs (see van Gils et al. 2003). In any case, the existence of this additional layer of physiological adjustment makes experimental analyses of the relationships between work level and work type, specific organ sizes and energy requirements more difficult (Bautista et al. 1998, Piersma 2002).

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References

- Battley, P. F. and Piersma, T. 2004. Adaptive interplay between feeding ecology and features of the digestive tract. – In: Starck, J. M. and Wang, T. (eds). *Adaptations in food processing and digestion in vertebrates*. – Enfield, USA.
- Battley, P. F., Dekinga, A., Dietz, M. W., Piersma, T., Tang, S. and Hulsman, K. 2001. Basal metabolic rate declines during long-distance migratory flight in great knots. – *Condor* 103: 838–845.
- Bautista, L. M., Tinbergen, J., Wiersma, P. and Kacelnik, A. 1998. Optimal foraging and beyond: how starlings cope with changes in food availability. – *Am. Nat.* 152: 543–561.
- Cherel, Y., Robin, J.-P. and Le Maho, Y. 1988. Physiology and biochemistry of long-term fasting in birds. – *Can. J. Zool.* 66: 159–166.
- Daan, S., Masman, D. and Groenewold, A. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. – *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 259: R333–R340.
- Deerenberg, C., Overkamp, G. J. F., Visser, G. H. and Daan, S. 1998. Compensation in resting metabolism for experimentally increased activity. – *J. Comp. Physiol. B* 168: 507–512.
- Dekinga, A., Dietz, M. W., Koolhaas, A. and Piersma, T. 2001. Time course and reversibility of changes in gizzards of red knots alternately eating hard and soft food. – *J. Exp. Biol.* 204: 2167–2173.
- Dietz, M. W., Dekinga, A., Piersma, T. and Verhulst, S. 1999a. Estimating organ size in small migrating shorebirds with ultrasonography: an intercalibration exercise. – *Physiol. Biochem. Zool.* 72: 28–37.
- Dietz, M. W., Piersma, T. and Dekinga, A. 1999b. Body-building without power training: endogenously regulated pectoral muscle hypertrophy in confined shorebirds. – *J. Exp. Biol.* 202: 2831–2837.
- Gessaman, J. A. 1987. Energetics. – In: Giron Pendleton, G. A., Millsap, B. A., Cline, K. W. and Bird, D. M. (eds). *Raptor management techniques manual*. National Wildlife Federation, Washington, D.C. pp. 289–320.
- Gessaman, J. A. and Nagy, K. A. 1988. Energy metabolism: errors in gas-exchange conversion factors. – *Physiol. Zool.* 61: 507–513.
- Hammond, K. A., Chappell, M. A., Cardullo, R. A., Lin, R. and Johnsen, T. R. 2000. The mechanistic basis of aerobic performance variation in red junglefowl. – *J. Exp. Biol.* 203: 2053–2064.
- Kersten, M., Bruinzeel, L. W., Wiersma, P. and Piersma, T. 1998. Reduced basal metabolic rate of migratory waders wintering in coastal Africa. – *Ardea* 86: 71–80.
- Kleiber, M. 1961. *The fire of life*. – John Wiley, New York.
- Lindström, Å. and Kvist, A. 1995. Maximum energy intake is proportional to basal metabolic rate in passerine birds. – *Proc. R. Soc. London B* 261: 337–343.
- McNab, B. K. 2002. *The physiological ecology of vertebrates. A view from energetics*. – Cornell University Press, Ithaca.
- Piersma, T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. – *Integ. Comp. Biol.* 42: 51–67.
- Piersma, T., Koolhaas, A. and Dekinga, A. 1993. Interactions between stomach structure and diet choice in shorebirds. – *Auk* 110: 552–564.
- Piersma, T., Cadée, N. and Daan, S. 1995. Seasonality in basal metabolic rate and conductance in a long-distance migrant shorebird the knot. – *J. Comp. Physiol. B* 165: 37–45.
- Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., van der Meer, J. and Wiersma, P. 1996. Variability in basal metabolic rate of a long-distance migrant shorebird (red knot, *Calidris canutus*) reflects shifts in organ sizes. – *Physiol. Zool.* 69: 191–217.
- Reinertsen, R. E. 1983. Nocturnal hypothermia and its energetic significance for small birds living in arctic and subarctic regions. A review. – *Polar Res.* 1: 269–284.
- Speakman, J. R., Visser, G. H., Ward, S. and Król, E. 2001. The isotope dilution method for the evaluation of body composition. – In: Speakman, J. R. (ed.). *Body composition of animals. A handbook of non-destructive methods*. Cambridge University Press, Cambridge, pp. 56–98.
- Stokkan, K.-A. 1994. Hormone mechanisms involved in the preparation for cold in birds. – *J. Ornithol.* 135: 380.
- van Gils, J. A., Piersma, T., Dekinga, A. and Dietz, M. W. 2003. Cost-benefit analysis of mollusc-eating in a shorebird. II. Optimizing gizzard size in the face of seasonal demands. – *J. Exp. Biol.* 206: 3369–3380.
- Visser, G. H., Boon, P. E. and Meijer, H. A. J. 2002a. Validation of the doubly labelled water method in Japanese quail *Coturnix c. japonica* chicks: is there an effect of growth rate? – *J. Comp. Biol.* 170: 365–372.
- Visser, G. H., Dekinga, A., Achterkamp, B. and Piersma, T. 2000b. Ingested water equilibrates isotopically with the body water pool of a shorebird with unrivaled water fluxes. – *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 279: R1795–R1804.

- Weber, T. P. and Piersma, T. 1996. Basal metabolic rate and the mass of tissues differing in metabolic scope: migration-related covariation between individual knots *Calidris canutus*. – J. Avian Biol. 27: 215–224.
- Williams, J. B. and Tieleman, B. I. 2000. Flexibility in basal metabolic rate and evaporative water loss among hoopoe larks exposed to different environmental temperatures. – J. Exp. Biol. 203: 3153–3159.
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